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Potential exposure of a classical biological control agent of the soybean aphid, *Aphis glycines*, on non-target aphids in North America

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Abstract In summer 2007, the Asian parasitoid *Binodoxys communis* (Hymenoptera: Braconidae) was released in North America for control of the exotic soybean aphid, *Aphis glycines* (Hemiptera: Aphididae). Despite its comparatively narrow host range, releases of *B. communis* may still constitute a risk to native aphid species. To estimate the risk of exposure of non-target aphids to *B. communis*, we merged assessments of temporal co-occurrence with projections of spatial overlap between *B. communis* and three native aphid species, and in-field measurements of the incidence of ecological filters that may protect these aphids from parasitism. Temporal co-occurrence was assessed between *A. glycines* and native aphids (*Aphis asclepiadis*, *Aphis oestlundi*, and *Aphis monardae*) at four different locations in Minnesota, USA. The degree of temporal overlap depended greatly on location and aphid species, ranging between 0 and 100%. All of the native aphids were tended by multiple species of ants, with overall ant-attendance ranging from 26.1 to 89.6%. During temporal overlap with *A. glycines*, $53 \pm 11\%$ of *A. monardae* colonies were partly found in flower heads of their host plant, with flowers acting as a physical refuge for this aphid. The extent of geographic overlap between *B. communis* and native aphids based upon Climex modeling was 17–28% for *A. monardae*, 13–22% for *A. oestlundi*, 46–55% for *A. asclepiadis* and 12–24% for the *A. asclepiadis* species complex. The estimated overall probability of potential exposure of *B. communis* on native aphids was relatively low ($P = 0.115$) for *A. oestlundi* and high ($P = 0.550$) for *A. asclepiades*. Physical and ant-mediated refuges considerably lowered probability of population-level impact on *A. monardae*, and could lead to substantial reduction of exposure for the other native aphids. These findings are used to make broader statements regarding the ecological safety of current *B. communis* releases and their potential impact on native aphid species in North America.

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Introduction

Classical biological control, the intentional release of exotic natural enemies to suppress pests or weeds, can reduce pest or weed problems and associated pesticide use. However, this strategy may also pose a risk to indigenous species and threaten the integrity of biological communities (Follett and Duan 2000; Wajnberg et al. 2001; Louda et al. 2003; Kimberling 2004; Bigler et al. 2006). For arthropod biological control in particular, risk to native species has often remained undefined and ecological safety has only received major attention during the past decade (Jewel et al. 1999; Strong and Pemberton 2001; van Lenteren et al. 2006). Laboratory host-specificity tests, the cornerstone of current prerelease risk assessment, may fail to predict the magnitude of non-target risk to native species (Louda et al. 2003; Van Driesche and Reardon 2004). As a complement to these tests, several aspects of species ecology have received increased attention, and the value of food-web analyses and community-assemblage studies has been stressed recently (Brodeur and Rosenheim 2000; Strong and Pemberton 2001; Pearson and Callaway 2005; Willis and Memmott 2005; Messing et al. 2006). These studies can provide robust predictive tools that are improving risk assessment for arthropod biological control (Messing and Wright 2006).

Methods for quantifying the magnitude and spatio-temporal scale of impact of exotic natural enemies on entire populations of native insects are crucial to advance current risk assessment (Hopper 2001; Babendreier et al. 2005; Wright et al. 2005). Barlow et al. (2004) indicated that estimation of population-level impact depends greatly on knowledge of non-target host biology and population dynamics. Understanding selected ecological attributes of native communities can also help to estimate the exposure of non-target organisms to biological control agents (Levine and D'Antonio 1999; Dzialowski et al. 2007). Exposure analysis is an integral aspect of ecological risk assessment as outlined by the United States Environmental Protection Agency (US EPA 1998) but it is rarely explicitly investigated in arthropod biological control projects. Pioneering work on potential non-target impacts of *Trichogramma* parasitoids, however, has shown that such studies are feasible and can yield important insights (Andow et al. 1995; Babendreier et al. 2003; Kuske et al.

2004; Wright et al. 2005). Additionally, a number of studies in both weed and arthropod biological control have shown that geographic and temporal differences in overlap between biological control agents and non-target species can greatly influence the overall risk to non-targets (e.g. Barratt et al. 2000; Pemberton 2000; Follett et al. 2000).

Pre-release assessment of spatial overlap of released exotics with native species hinges upon proper delineation of their respective geographic distributions. Modeling species distribution has become important in various scientific disciplines such as conservation biology (Anderson and Martinez-Meyer 2004), invasion biology (Drake and Lodge 2006) and biological control (Goolsby et al. 2005; Fiaboe et al. 2006). Insights into species distribution can help quantify risk, defined as the product of exposure (i.e., spatial overlap) and a hazard index related to species vulnerability to a stressor (e.g., a released biological control agent) (Allen et al. 2006). Modeling outcomes can then complement laboratory and field data in probabilistic risk assessment (Wright et al. 2005).

The soybean aphid, *Aphis glycines* Matsumura, is a target for classical biological control in North America (Heimpel et al. 2004; Wyckhuys et al. 2007a). An invasive species from Asia, *A. glycines* has become a destructive pest of soybean in both the U.S. and Canada since its initial discovery in 2000 (Ragsdale et al. 2004, 2007). After intensive quarantine testing, the Asian aphidiine braconid *Binodoxys communis* (Gahan) was permitted for release against *A. glycines* in summer 2007. Laboratory studies have shown that *B. communis* maintains a relatively narrow host range that includes some non-target aphid species which are native to North America (N. Desneux and G.E. Heimpel, unpublished; Wyckhuys and Heimpel 2007).

Previous work in our laboratory has shown that some native aphid species are likely protected from *B. communis* attack through ant-tending and physical refuges (Wyckhuys et al. 2007b). However, the incidence of these ecological filters in their natural environments is not yet quantified. Also, although various facets of *B. communis* biology and ecology have been revealed (e.g., Yu et al. 2005; Wyckhuys et al. 2008a, b), information is lacking on phenology and spatial distribution of North American aphid species that this parasitoid is capable of successfully attacking in the laboratory. Merging these insights with projections of *B. communis* spatiotemporal

occurrence as part of an overall exposure analysis will help make ecological risk assessment for *A. glycines* biological control meaningful and predictive.

Here, we compare temporal patterns of *A. glycines* abundance with those of three native aphid species. We also quantify incidence of certain ecological filters (i.e., ant-mediated and physical refuges) in the natural habitats of these aphids. Next, potential spatial co-occurrence of *B. communis* with native aphids is determined by linking (predicted) parasitoid distribution with native aphid distribution in North America. Lastly, we combine projections on spatial co-occurrence with data on temporal overlap, parasitism and extent of protection (through refuges) to define likelihood of potential exposure.

Materials and methods

Temporal patterns in aphid abundance

A total of four different aphid species were monitored throughout the state of Minnesota, USA during May–October 2006. We studied *A. glycines* populations in soybean fields at Saint Paul (44°59′25″ N, 93°10′25″ W), Rosemount (44°42′38″ N, 93°4′55″ W), Austin (43°40′47″N, 92°53′8″ W) and Lamberton (44°10′6″ N, 95°14′43″ W). Fields were visited from soybean emergence (late May–early June) until plant senescence (mid-September). Initially, we inspected a total of 80 plants at each site for *A. glycines*. During the course of the cropping season, the number of inspected plants was gradually reduced to 20 or 40 at peak aphid densities during August. We counted the number of aphids per plant and recorded the presence of ants, aphid mummies and the level of ant-tending. Each field was visited on a 2-week basis, and it was ensured that no pest management practices were used.

We also monitored populations of *Aphis monardae* Oestlund, *Aphis oestlundi* Gilette and *Aphis asclepiadis* (Fitch) in mesic to wet-mesic prairie fragments. These aphid species are native to North America and were successfully parasitized by *B. communis* under laboratory conditions (N. Desneux and G.E. Heimpel, unpublished). The prairie sites included four Minnesota Department of Natural Resources Scientific and Natural Areas: River Terrace Prairie (44°32′4″ N, 92°48′31″ W), Iron Horse Prairie (43°52′1″ N, 92°50′49″ W),

Glynn Prairie (44°15′52″ N, 95°41′51″ W) and Holthe Prairie (43°44′32″ N, 95°3′46″ W), as well as the Cedar Creek Natural History Area (45°24′4″ N, 93°12′33″ W). Prairie sites were selected to be in close proximity to soybean fields, as to group them pair-wise based on location as follows: Saint Paul & Cedar Creek (North Central, NC), Rosemount & River Terrace (South Central, SC), Austin & Iron Horse (Southeast, SE) and Holthe, Glynn & Lamberton (Southwest, SW). Sampling locations were thereby grouped in four different regions of Minnesota. At each site, we monitored abundance of the various aphids on their respective summer host plants. We monitored *A. monardae* on wild bergamot *Monarda fistulosa* L. (Lamiaceae), *A. oestlundi* on evening primrose *Oenothera biennis* L. (Onagraceae) and *A. asclepiadis* on common milkweed *Asclepias syriaca* L. (Apocynaceae). These plant species are common members of prairie communities in central North America.

During each visit, we recorded the number of aphids on 75 randomly-selected individuals of each plant species. Some plant species were absent at certain sites (i.e., evening primrose in Holthe and Glynn) while they were uncommon at others. At sites where a certain plant was not commonly encountered, we monitored aphid abundance on only 25 plants. On plants with aphid colonies, we recorded the presence of ants, parasitoid mummies and ant-tending. Ants that were observed tending colonies of the different aphid species were collected for identification. Parasitoid mummies were collected and reared in 0.5 ml micro-centrifuge tubes, and emerged parasitoids were placed in 70% ethanol, dehydrated following Heraty and Hawks (1998), and point-mounted for identification by RRK. Parasitoid voucher specimens were deposited at the US National Museum of Natural History (Washington, DC) and at the University of Minnesota (Saint Paul). We also recorded the phenological stage of the host plant (i.e. flowering vs. vegetative) and whether *A. monardae* colonies aggregated in *M. fistulosa* flower heads. Wyckhuys et al. (2007b) found that *M. fistulosa* flower heads and attendance by ants may act as refuges against *B. communis*. Prairie sites were visited approximately every 2 weeks, with initial visits conducted in early to mid-May (i.e., prior to soybean planting).

Per location, we defined 'temporal overlap' of a given native aphid with *A. glycines* as the proportion of sampling events in which both the native species and

A. glycines were found, and the percentage *A. glycines*-infested soybeans was higher than the percentage of plants with the native species. This reasoning will be explained below, when describing the likelihood of *B. communis* spill-over from soybean fields. Parasitoids such as *B. communis* may pose the greatest risk to native aphid species at times when its key host, *A. glycines*, reaches high population levels and native aphid species occur at comparatively low densities (e.g., Rand and Louda 2006; Rand et al. 2006).

Predicted distribution of *B. communis*

A key determinant for establishment of a biological control agent is its adaptability to local environmental conditions (Bryne et al. 2002; Hoelmer and Kirk 2005; Goolsby et al. 2005). For this purpose, *B. communis* was collected from areas in Asia with climates comparable to major soybean-growing regions in North America (e.g., Venette and Ragsdale 2004). One strain of *B. communis* was collected during 2002 in the Chinese province of Heilongjiang, near the city of Harbin. Given the precise collection location of this specific *B. communis* strain, and the lack of reliable information regarding its geographic distribution in Asia, we used this location for further spatial modeling.

We used the 'Match Climates' function within the CLIMEX v2 software (Sutherst et al. 2004) to compare the climatic conditions of Harbin with those throughout North America. CLIMEX is an eco-climatic modeling package commonly used for predicting the geographic distribution of invasive species and exotic biological control agents (e.g., Goolsby et al. 2005; Dunlop et al. 2006). The software package uses databanks of historical weather data from numerous locations worldwide to match climates and map distributions of certain species. The level of climatic similarity is given by a 'Composite Match Index' (CMI), an average of seven indices that indicate the degree of similarity of maximum and minimum temperatures, total rainfall, rainfall pattern, relative humidity and soil moisture. Each of these indices can range between 0 and 100, with a value of 100 indicating an exact match between two locations.

Locations within North America with CMI $\geq$ 60, representing a climatic match of 60.0% or higher, were visualized within an ArcView environment. We used a fairly broad range of climatic suitability to

predict *B. communis* distribution in North America, partly because of uncertainty regarding the climate requirements of the released strain of this parasitoid. We designated a 150-km buffer around locations of potential *B. communis* establishment.

Geographic distribution of native aphids

To model the geographic distribution of the various native aphids, we used the Genetic Algorithm for Rule-Set Prediction (GARP; Stockwell and Peters 1999). GARP is a machine-learning approach that develops a set of conditional rules to relate species occurrence to a custom set of biotic and abiotic parameters. Species occurrence data are divided into two sets: (1) a randomly-selected data set used to train the model and formulate a rule to predict species presence and (2) a data set used to test the developed rules. The GARP algorithm is conceptualized to deal with presence-only data through automated selection of pseudo-absence localities from the study area. GARP is non-deterministic and develops a user-defined number of models, with subsequent runs producing somewhat different results. We used the Desktop GARP version and employed standard procedures for program implementation.

For each of the native aphid species, we obtained locality data from the published literature and museum records. We screened various entomology museums in North America with online-accessible databases, and obtained literature records from areas including Illinois, the Rocky Mountain Region, California, Texas, Nebraska and Manitoba (Canada) (Williams 1910; Essig 1917; Gillette and Palmer 1932; Palmer 1952; Mortimer and Tissot 1965; Rojanavongse and Robinson 1977). A minimum of 15 locality points were obtained per species, with all available records included in the analysis. As *A. asclepiadis* is regularly synonymyzed with the closely-related species *Aphis heraclella* Davis and *Aphis helianthi* Monell, we also obtained locality data for these species to delineate the distribution of the species complex (Palmer 1952; Addicott 1981; Cook 1984). Locality data for each aphid species as well as the *A. asclepiadis* complex were geo-referenced and entered into Desktop GARP. We also used a set of ecological and climate variables as input for the prediction. These variables were available within Desktop GARP, at a North American grid with 0.2°

square cells (Phillips et al. 2004). We incorporated maps of eight different environmental variables: annual precipitation, elevation, slope, aspect, average daily temperature, temperature range and number of wet days. Aspect refers to the direction to which a mountain slopes. Climate variables are derived from weather station readings during the period 1961–1990 (New et al. 1999), while the remaining datasets were derived from a digital elevation model. For each aphid species and the *A. asclepiadis* complex, we allowed GARP to produce a total of 20 models. For each run, we used half of the species localities for training, with a convergence limit of 0.01 and a maximum of 1,000 iterations.

The final GARP model combined results from the 20 different models, yielding an indication of the likelihood that a certain aphid species or the *A. asclepiadis* complex is present at a given location. Data were entered into ArcView and projected onto a map of North America. In the resultant maps, pixels had values ranging from zero (i.e., no models predicted presence of a given aphid species) to 20 (i.e., all models predict presence). For model evaluation, we carried out Chi-Square tests, comparing prediction efficiency of independent extrinsic test data between GARP model predictions and random models (Peterson 2001).

Geographic overlap and probabilistic risk assessment

To estimate the potential geographic overlap of *B. communis* with native aphids throughout North America, we developed overlay maps of potential parasitoid distribution with delineated geographic distribution of each aphid species or the *A. asclepiadis* complex. However, the impact of *B. communis* on native aphids depends not only on the presence of its key host, *Aphis glycines*, but is also mediated by the likelihood of parasitoid drift (Follett et al. 2000). Through this process, *B. communis* could develop new associations with other aphid hosts throughout its region of climatic suitability. To quantify the extent of spatial overlap, we considered two different scenarios: (A) *B. communis* only expands its host range in areas with high *A. glycines* abundance through passive spillover from soybean fields to nearby natural areas (e.g., Rand and Louda 2006), and (B) *B. communis* develops new associations with non-target aphids and

poses a risk to native aphids throughout a broader region of climatic suitability (e.g., Follett et al. 2000). For scenario A, we mapped records of *A. glycines* outbreaks during the past six years throughout North America (NAPIS 2006; Venette and Ragsdale 2004). For scenario B, we used the predicted geographic distribution of *B. communis* based on climatic similarity.

For each of the native aphids, we developed decision trees to evaluate the probability of *B. communis* potential exposure on their respective populations. Decision trees are widely used in risk assessment and describe the probability that certain contingencies occur, with probabilities multiplicative along the 'branches' of the tree (e.g., Wright et al. 2005). For scenario A, we developed decision trees for each native aphid based on two contingencies: extent of temporal overlap and degree of spatial overlap. Extent of temporal overlap was averaged for each of the four locations. For *A. monardae*, we refined decision trees by incorporating the degree of ant-attendance and aggregation in *M. fistulosa* flower heads. Both measures were calculated during times when the proportion of *A. glycines*-infested plants surpassed that of plants with native aphids (i.e., highest likelihood of spillover). The degree of ant-attendance was corrected for the proportion of the ant *Lasius neoniger* (Emery) within samples of aphid-tending ants. In laboratory trials, *L. neoniger* significantly lowered *B. communis* parasitism of *A. monardae* (Wyckhuys et al. 2007b).

Results

Temporal patterns in aphid abundance

Population dynamics of *A. glycines* and native aphids differed greatly between the various locations (Fig. 1). In the Central region, we first found *A. glycines* in soybean fields in early June, while its first reports in the Southwest and Southeast were at the end of June or in mid-July. At all locations, *A. glycines* was found on all plants during some part of the season. Peak *A. glycines* density (mean ± sd/plant) was reached on July 5 (311.6 ± 59.2; North Central), July 27 (115.3 ± 21.4; South Central), August 23 (319.0 ± 30.7; Southwest) and August 16 (815.0 ± 204.0; Southeast). No parasitoid mummies were found. In the North Central region, we found one *A. glycines* colony tended by *L. neoniger* on
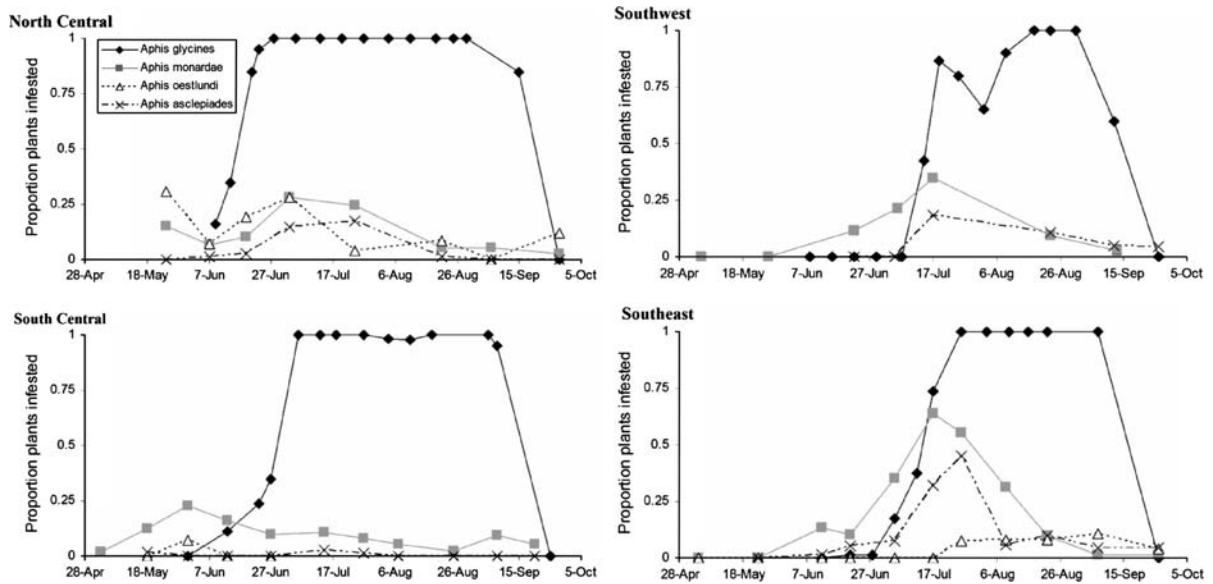
Fig. 1 Temporal patterns in abundance of soybean aphid (*A. glycines*) and three native aphid species (*A. monardae*, *A. oestlundi* and *A. asclepiadis*) on their respective summer hosts.

Patterns are represented for four different locations, indicated per region, throughout Minnesota, USA. Abundance is indicated as proportion of plants infested by the respective aphids

July 9, while aphid-tending ants were not found in the other regions.

Among the native aphids, *A. monardae* was most commonly found, with maximum incidence ranging from 0.23 to 0.64 fraction of host plants infested. Various aphid species attained peak levels prior to arrival of *A. glycines* in soybean fields. Average *A. monardae* colony sizes were 56.9 ± 13.3 (North Central), 21.8 ± 14.1 (South Central), 29.1 ± 20.8 (Southwest) and 27.9 ± 23.4 (Southeast). For *A. oestlundi*, average colony sizes were 145.6 ± 147.4 (North Central), 72.0 ± 0.0 (South Central) and 17.7 ± 21.3 (Southeast). We did not find any *A. oestlundi* colonies in the Southwest region. Average *A. asclepiadis* colony sizes were 64.1 ± 87.8 (North Central), 1.5 ± 1.3 (South Central), 48.1 ± 37.0 (Southwest) and 255.3 ± 458.8 (Southeast).

The degree of temporal overlap between native aphids and *A. glycines* depended greatly on location. Overlap with *A. monardae* was 100.0% (North Central), 64.0% (South Central), 60.0% (Southwest) and 56.0% (Southeast). Populations of *A. oestlundi* temporally overlapped with *A. glycines* for 86.0% (North Central), 0.0% (South Central) and 80.0% (Southeast). The degree of temporal overlap with *A. asclepiadis* was 100.0% (North Central), 67.0% (South Central), 75.0% (Southwest) and 67.0% (Southeast).

A total of 16 different ant species were found in association with *Aphis monardae* colonies, while *A. oestlundi* and *A. asclepiadis* were tended by five and eight species, respectively (Table 1). The level of ant attendance differed greatly, depending on aphid species and location. For *A. monardae*, the degree of ant tending was 63.5% (North Central), 56.5% (South Central), 33.3% (Southwest), 45% (Southeast) of all colonies. For *A. oestlundi*, the degree of ant tending was 26.1% (North Central), 75.0% (South Central) and 30.0% (Southeast). For *A. asclepiadis*, the degree of ant tending was 64.3% (North Central), 50.0% (South Central), 89.6% (Southwest) and 60.0% (Southeast). The level of ant tending on *A. monardae* colonies also showed great temporal fluctuations (Fig. 2). During temporal overlap with *A. glycines*, the degree of ant-attendance on *A. monardae* ranged from 32.9% (Southwest) to 66.1% (North Central). The ant *L. neoniger* constituted 27.0% of the *A. monardae*-tending ant complex.

Flowering *M. fistulosa* were found during July 3–24 (North Central), July 14–August 25 (South Central), July 6–17 (Southwest) and July 5–26 (Southeast). These time periods covered $22.0 \pm 15.0\%$ of temporal overlap between *A. glycines* and *A. monardae*. During this time period, 57.0, 42.0, 67.0 and 45.0% of *A. monardae* colonies were found on

Table 1 Ant species found in association with *A. monardae*, *A. oestlundi* and *A. asclepiadis* during May–September 2006 at four different locations in Minnesota, USA

Ant species	*Aphis monardae*				*Aphis oestlundi*			*Aphis asclepiadis*		
	SE	SW	SC	NC	SE	SC	NC	SE	SW	NC
Camponotus novaeboracensis (Fitch)			2							
Crematogaster cerasi Fitch	1		1							
Formica incerta Emery			2							
Formica knighti Buren									1	
Formica lasioides Emery				5						
Formica montana Emery		2								2
Formica neonagates Emery				1	1					
Formica obscuripes Forel			2				3	1		
Formica subsericea Say	1		4	1					2	1
Formica vinculans Wheeler			1							
Lasius alienus Mayr			1		1			1		
Lasius neoniger Emery	11	3			2	1		4	1	1
Monomorium minimum Buckley			2							
Myrmica cf americana Weber			2				1			
Myrmica n sp. Francoeur							1			
Myrmica lobifrons Pergande			1							
Prenolepis imparis (Say)			2							1
Temnothorax ambiguous Emery	1		1							
Total	14	5	21	11	3	1	5	5	6	5

Numbers indicate the total number of individuals of a given species that were collected for identification from different aphid colonies. Locations are: Southeast (SE), Southwest (SW), South Central (SC) and North Central (NC)
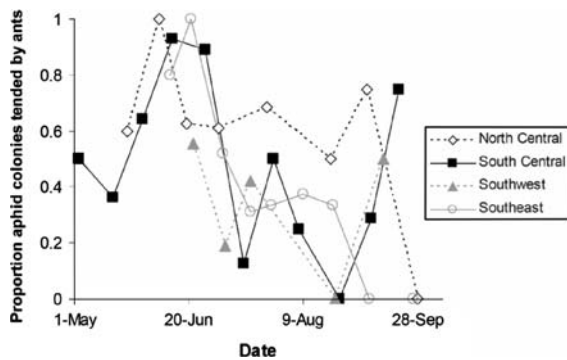
Fig. 2 Proportion of *Aphis monardae* colonies tended by ants during May–September 2006 at four different locations in Minnesota, USA. The locations are represented by region (North Central, South Central, Southwest and Southeast). Dates of the various sampling events are indicated, with omission of dates on which no *A. monardae* colonies were found

flowering plants in the North Central, South Central, Southwest and Southeast region, respectively. Between 35.0% (Southeast) and 62.5% (North Central) of aphid colonies on flowering plants were tended by ants. On flowering plants, aphids were mainly found within the flower head.

Parasitoid mummies were recorded from 1.4% (North Central), 6.5% (South Central), 0.0% (Southwest) and 12.6% (Southeast) of *A. monardae* colonies. One parasitoid mummy was also found in an *A. asclepiadis* colony in the Southwest region. All mummies yielded the native, generalist, primary parasitoid *Lysiphlebus testaceipes* (Cresson).
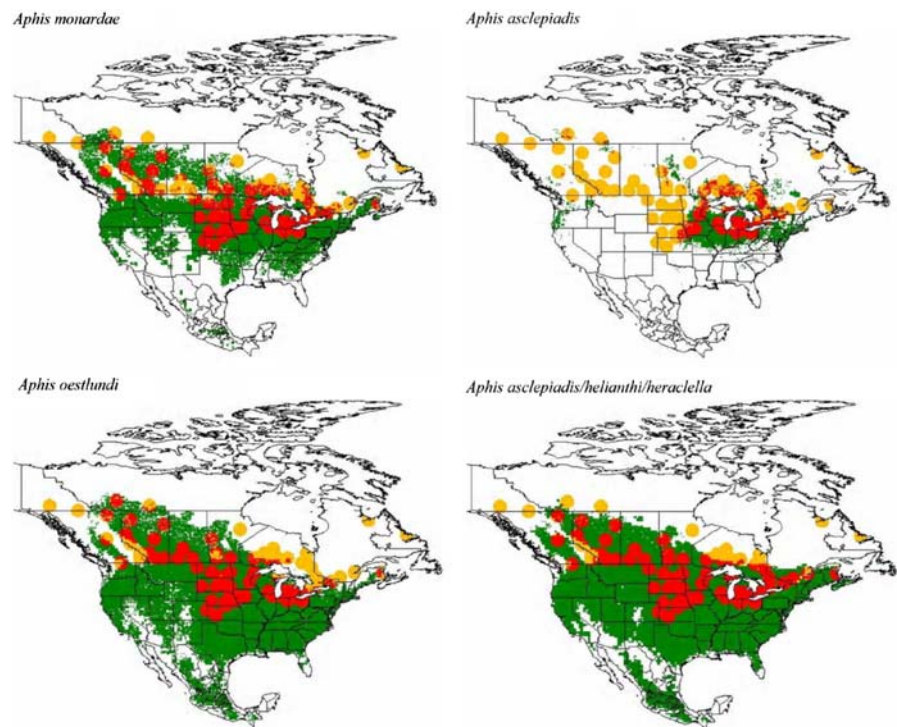
Predicted distribution of *B. communis*

The degree of climatic similarity between Harbin (China) and locales throughout North America showed great variability. Maximum CMI scores were 80 and were reported for 12 locations: North Dakota, USA (four) Alberta (one), Manitoba (three), Ontario (one), and Saskatchewan (three) (Canada). The range of locales with CMI ≥ 60 covered the Central region of the US and several Canadian provinces (Fig. 3).

Geographic distribution native aphids

We obtained a total of 23 locality points for *A. monardae*, 34 for *A. oestlundi*, 14 for *A. asclepiadis*, 49 for *A. helianthi* and 17 for *A. heraclella*. In

general, GARP models for the various aphid species were highly significant. Chi-Square tests showed higher prediction efficiency for the multiple GARP models—computed for each species—than for random models, with $0.13 \leq P \leq 2.92 \times 10^{-7}$ for *A. monardae*, $0.07 \leq P \leq 2.73 \times 10^{-6}$ for *A. oestlundi*, $0.02 \leq P \leq 2.12 \times 10^{-17}$ for *A. asclepiadis* and $4.44 \times 10^{-6} \leq P \leq 1.30 \times 10^{-16}$ for the *A. asclepiadis* complex. For *A. monardae*, the highest probability of species occurrence was recorded throughout the northern part of the USA, from Oregon to New England (Fig. 4). Distribution maps of *A. oestlundi* covered most of the US and the Central Canadian provinces. Areas where GARP predicted the highest probability of *A. asclepiadis* presence were basically restricted to the North Central region of the US, in close vicinity of its locality points. However, the *A. asclepiadis* complex was predicted to occur throughout the USA and most Canadian provinces.

Spatial overlap and probabilistic risk assessment

For scenario A (spillover only), areas with *A. glycines* presence overlapped to differing extents with the distribution of each of the native aphid species/ complexes (Fig. 5). The extent of spatial overlap was 17.2% for *A. monardae*, 13.4% for *A. oestlundi*, 55.2% for *A. asclepiadis* and 12.8% for the *A. asclepiadis* species complex. For scenario B (ecosystem infiltration limited by parasitoid climatic tolerance), the extent of spatial overlap with *B. communis* was 27.5% for *A. monardae*, 21.7% for *A. oestlundi*, 46.4% for *A. asclepiadis* and 24.3% for the *A. asclepiadis* species complex. Lack of (predicted) co-occurrence of *A. asclepiadis* and *B. communis* was noted in Illinois, southern Indiana, northern Missouri and the entire East Coast.

Data on spatial and temporal overlap were used to construct decision trees for each native aphid species (Table 2). The potential for exposure of non-target aphids to *B. communis* was relatively low for *A. oestlundi* and the *A. asclepiadis* complex. Incorporation of the protective role of aphid-tending by *L. neoniger* and aggregation in flower heads yielded lower potential exposure of *A. monardae*.

Discussion

Aphids take part in various ecological processes and are important constituents of arthropod food webs in many natural ecosystems. Zoebelein ([1956](#)) recorded

Fig. 4 Modeled distribution for *A. monardae*, *A. oestlundi*, *A. asclepiadis* and the *A. asclepiadis/helianthi/ heraclella* complex. Each color reflects the number of GARP models that predict presence of a given aphid species. Darker colors indicate a higher fraction (out of 20) of GARP models predicting presence of the different aphid species and complexes. Reported locality points for each aphid species are indicated as blue dots
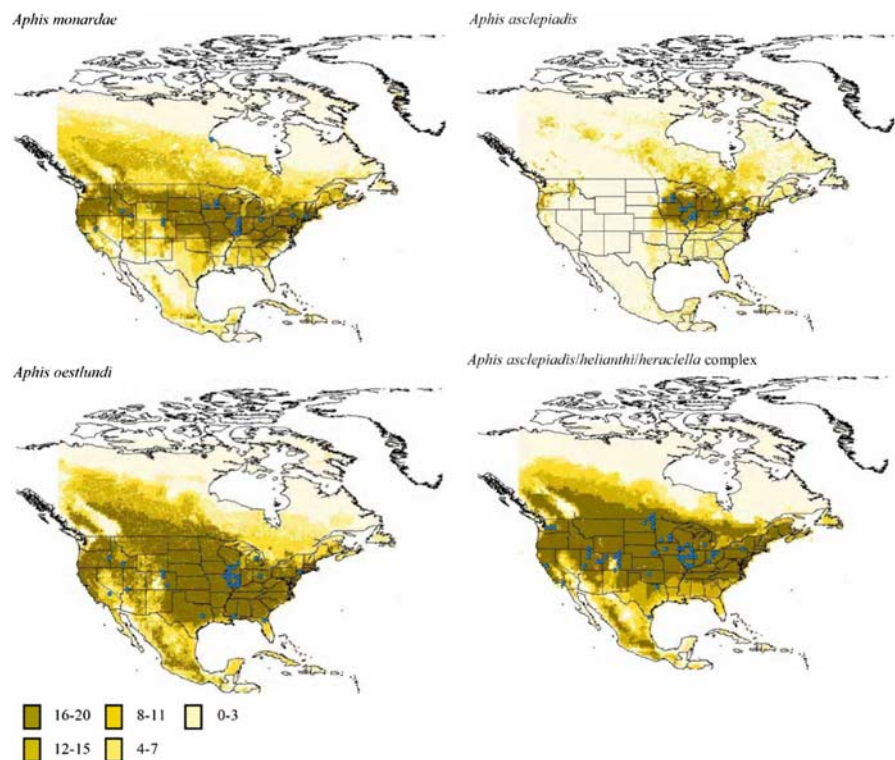

Fig. 5 Spatial overlap between known *A. glycines* distribution and modeled distribution maps for *A. monardae*, *A. oestlundi*, *A. asclepiadis* and the *A. asclepiadis/helianthi/ heraclella* complex. Soybean aphid distribution is indicated in orange. Native aphid distribution (green areas) show locations where >50% GARP models predict presence of a given aphid species or complex. Red colors indicate an overlap of the distribution of *A. glycines* and respective native aphids. Scenario A was based on this situation
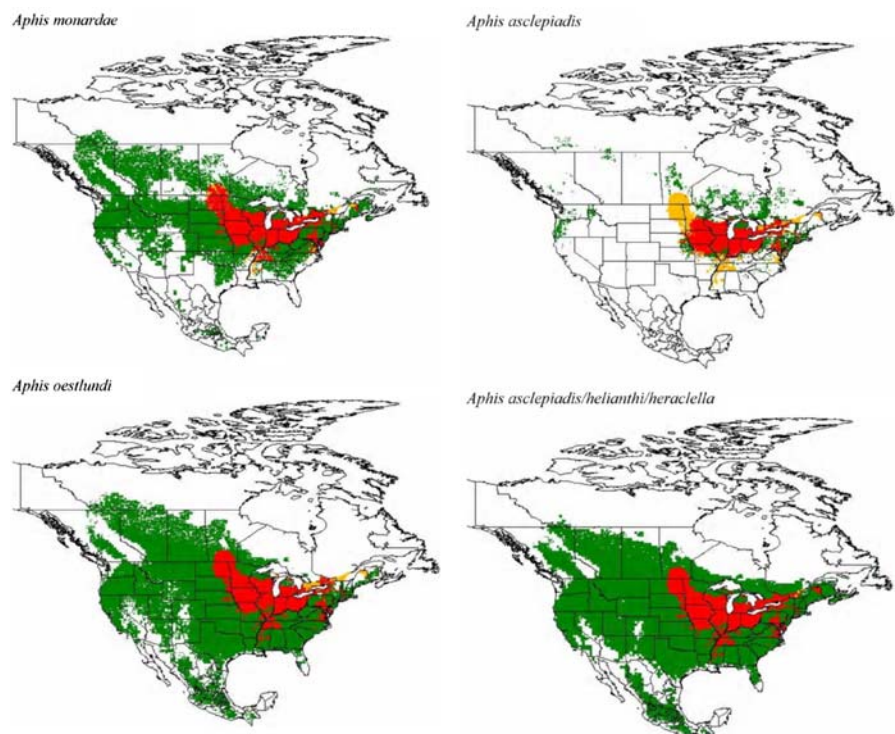
Table 2 Potential exposure of native aphid species (complexes) in North America to released *B. communis*, as caused by parasitoid spillover from soybean fields with *A. glycines* outbreaks (scenario A)

Native aphid species	Contingency	Average probability	Estimate of potential exposure	
			P	Worst case *P**
Aphis oestlundi	Spatial overlap	0.13	–	–
	Temporal overlap	0.55	**0.073**	**0.115**
	Unprotected by ants[a]	*0.56*	*0.041*	*0.085*
Aphis asclepiadis	Spatial overlap	0.55	–	–
	Temporal overlap	0.77	**0.425**	**0.550**
	Unprotected by ants	*0.34*	*0.144*	*0.275*
Aphis asclepiadis complex	Spatial overlap	0.13	–	–
	Temporal overlap	0.77	**0.098**	**0.128**
	Unprotected by ants	*0.34*	*0.033*	*0.064*
Aphis monardae	Spatial overlap	0.17	–	–
	Temporal overlap	0.70	0.119	0.172
	Unprotected by ants (corrected for *L. neoniger*)[b]	0.88	0.105	0.158
	Occurring outside of *M. fistulosa* flower heads	0.62	**0.065**	**0.132**

Final estimates (indicated in bold) are products of the discrete probabilities of the appropriate contingencies. *P*-values were obtained through modeling spatial overlap between *B. communis* and the various native aphids as well as on field work conducted at four locations in Minnesota, USA

* Worst case scenario probability was estimated by using maximum temporal overlap, minimum extent of ant-tending or lowest number *A. monardae* colonies on *M. fistulosa* flowerheads (out of the four different locations)

[a] Ant protection is indicated as a separate contingency for *A. asclepiadis*, *A. oestlundi* and the *A. asclepiadis* complex despite lack of information for these species on the degree of protection against *B. communis* parasitism provided by ants

[b] Only *L. neoniger* was included as protection of *A. monardae* colonies against parasitism was only observed for this species. For ease of computation, the proportion of *L. neoniger* within the *A. monardae*-tending ant community was kept constant for the various locations

256 insect species in a natural habitat that directly consume honeydew produced by hemipterans such as aphids, while ant-aphid mutualisms are termed keystone interactions that shape the structure of natural communities (Styrsky and Eubanks 2007). A major perturbation of aphid assemblages and their interacting species could lead to a cascade of community-level effects (Schreiner and Nafus 1992; Simberloff and Stiling 1996; Heimpel et al. 2004). Therefore, the release of an exotic parasitoid such as *B. communis* and its associated risks to native aphids should receive scrutiny. This study provides insights into aphid phenology, geographical distribution and community linkages, which complement the current state of knowledge on native aphids in North America. Projections of temporal and spatial co-occurrence of *B. communis* with native aphids allow for quantitative assessment of the potential exposure of non-target aphids to *B. communis*.

Temporal overlap determined the probability of potential exposure of native aphids to *B. communis* to varying extent for the different aphid species. However, the potential impact of *B. communis* does not exclusively depend on temporal overlap between *A. glycines* and non-target aphids, but also on emergence patterns and ecology of *B. communis*. Studies of temperature-dependent development of *B. communis* led to a prediction of emergence during early- to mid-May in various parts of the Midwest (S. Acheampong, K. Wyckhuys, G.E. Heimpel, unpublished) suggesting that exposure of non-target species could occur prior to appearance of *A. glycines* on soybean. Many of the native aphid species in our study were present before soybeans were planted in Minnesota. For example, *A. monardae* attained peak incidence of 23.0% plants infested in the South Central region of Minnesota 2 weeks prior to the first records of *A. glycines* in soybean plots. Although *B. communis* may emerge in May in Minnesota, parasitoids may still occur at low abundance levels and therefore constitute low risk to aphids during this time. This is somewhat illustrated by the virtual

absence of the native parasitoid *L. testaceipes* from the native aphid community, especially during early summer despite similar degree-day requirements for development (S. Acheampong, K. Wyckhuys and G.E. Heimpel, unpublished).

Low abundance of *L. testaceipes* in prairie habitats may also be related to high levels of ant tending of its aphid hosts. All three native aphids (*A. monardae*, *A. asclepiadis* and *A. oestlundi*) maintained strong community linkages, being tended by a diverse and abundant ant complex. Aphid-tending ants commonly reduce the survival and abundance and also alter the spatial distribution of aphid natural enemies (e.g., Renault et al. 2005; Styrsky and Eubanks 2007). Wyckhuys et al. (2007b) indicated that the ant *L. neoniger* considerably lowered parasitism of *A. monardae* by *B. communis*. Although *L. neoniger* tended all three aphid species and was the most common ant in our study, it did not occur equally in all locations. As ant species differ greatly in their degree of aggressiveness (Hubner 2000; Kaneko 2003), we cannot assume the same level of protection by all ant species as provided by *L. neoniger* (for *A. monardae*). Also, myrmecophily does not necessarily lead to protection of aphids against parasitism, with certain parasitoids foraging successfully in ant-tended aphid colonies (Stary 1966; Liepert and Dettner 1996; Völkl and Novak 1997).

The association of *A. monardae* colonies with *L. neoniger* would likely cause sharp reductions in the exposure of native aphids to *B. communis*. High levels of myrmecophily in natural habitats very likely translate into strong biotic resistance against *B. communis*. Thus, interaction between native aphids and a diverse range of (potential) predators could safeguard the integrity of these native communities (Crawley 1986; Schoener and Spiller 1995; Miller et al. 2002).

Potential exposure measures for each of the native aphids were also greatly determined by the degree of spatial overlap between (forecasted) *B. communis* distribution and delineated distribution of native aphids. In both the spillover and ecosystem-infiltration scenarios, *A. monardae* and *A. oestlundi* benefited greatly from occurring in geographical regions where *B. communis* is less likely to become present. Such regions may constitute geographical refuges for both species (Follett et al. 2000; Louda et al. 2003). In the meantime, high spatial overlap of *A. asclepiadis* with

B. communis may place this species at elevated risk of exposure. Additionally, it should be stressed that *A. asclepiadis* (kept on *Asclepias* spp. host plants) and *A. oestlundi* are suboptimal hosts for *B. communis*, with most wasps unsuccessfully developing on these species (N. Desneux and G.E. Haimpel, unpublished). Lastly, our findings of spatial overlap hinge upon the accuracy of projections regarding species distributions.

Modeling species distribution based either on climatic similarity or on small numbers of occurrence records is somewhat controversial (Phillips et al. 2004; Stockman et al. 2006). Nevertheless, Stockwell and Peterson (2002) indicate that the accuracy of predicting species occurrence can be 90% within 10 sample points. Also, Dunlop et al. (2006) modeled the distribution of cold-tolerant ecotypes of the invasive weed *Senna obtusifolia* based upon a limited number of distribution records. Climate matching has also come under fire as not being an accurate basis for predicting species establishment (e.g., Hart et al. 2002). However, see Goolsby et al. (2005) for fairly strong parallels between CLIMEX CMI-indices and parasitoid establishment. One could argue that species are likely to establish in homologous climates but even more so in milder climates. In our case, this would mean that *B. communis* may easily establish in southern US states if suitable hosts would be present. Given these caveats, we strongly emphasize the need for retrospective analyses following *B. communis* release in North America. These should provide the opportunity to validate our models and eventually improve procedures for use in future biological control programs.

Predicted aphid distribution, as modeled by GARP, is not only affected by the set of ecological and climate variables used, but also depends on presence of suitable host plants. However, host use likely did not restrict aphid geographical distribution much, as all native aphids were found on a wide range of hosts. *Aphis monardae* has been reported from five hosts within the genera *Monarda* and *Myosotis*, *A. asclepiadis* from 17 host species, *A. helianthi* from 28 and *A. heraclella* from seven different hosts. Although *A. oestlundi* is only reported from two host plants; *O. biennis* and *Oenothera villosa* Thunb. spp. *strigosa* (Rydb.) W. Dietr. & Raven, these plants occur throughout the U.S (PLANTS Database 2007).

By focusing on potential exposure through spillover from soybean fields in scenario A, we did not intend to

infer lower likelihood of *B. communis* drift and subsequent establishment in a broader geographical area. Nevertheless, uncertainty on certain aspects of *B. communis* behavior and ecology only allows us to make ambiguous statements about spillover. In the event *B. communis* successfully establishes upon release, it will be most likely that agriculturally-subsidized parasitoids affect aphid populations in natural ecosystems adjacent to soybean plots (Rand and Louda 2006). Likelihood of parasitoid drift and of *B. communis* developing novel associations with nontarget aphids throughout its range of climatic suitability remains extremely difficult to predict (e.g., Secord and Kareiva 1996). Wyckhuys and Heimpel (2007) indicated that *B. communis* employs high levels of behavioral plasticity and orients towards a range of host-associated volatiles. This may hint at a lower likelihood that *B. communis* host foraging processes restrict its ecological host range and make drift more likely. Aside from info-chemicals mediating field host use, the potential impact of *B. communis* on aphid populations in natural habitats depends on its foraging efficacy in environments of differing architectural complexity (e.g., Babendreier et al. 2003; Wright et al. 2005). Research is ongoing to estimate *B. communis* habitat use and fidelity in its areas of endemism (L.M. Wang, K. Wyckhuys, K.M. Wu and G.E. Heimpel, unpublished) and will be incorporated into probabilistic risk assessment for this species.

We need to indicate that non-target species can also serve as a useful reservoir of hosts during times when target hosts are at low densities or unavailable (e.g., Murdoch et al. 1985; Nechols et al. 1992). Presence of suitable aphid hosts in prairie fragments embedded within soybean/corn monoscapes could benefit parasitoid establishment and the efficacy of *B. communis* for *A. glycines* biological control (e.g., Doutt et al. 1976; van Lenteren et al. 2006), thus leading to a trade-off between efficacy and safety of biological control.

The approach described in this manuscript complements laboratory-based host specificity studies that led to initial selection of a relatively host-specific specific strain of *B. communis* (N. Desneux and G.E. Heimpel, unpublished; Wyckhuys et al. 2007a) by estimating the magnitude or spatiotemporal scale of overlap of this parasitoid on native insect populations. Our goal was to provide a more comprehensive assessment of ecological risk of *B. communis* release. Although we did identify substantial potential for spatial and temporal

co-occurrence between *B. communis* and *A. asclepiades*, the community-linkages (i.e., ant tending) that we documented are likely to reduce the exposure of native aphids to *B. communis*. The comparatively narrow host range of *B. communis* (as determined through laboratory studies), combined with substantial geographical refuges and availability of ecological filters suggest a low overall risk to native aphid species. Other factors that remain unstudied and that may reduce risk further are habitat specificity and intra-guild predation (Chacon et al. in press). And lastly, the ecological risks posed to native aphids by a *B. communis* release could be outweighed by ecological benefits if biological control is successful in reducing insecticide applications or other negative consequences of the soybean aphid invasion (Heimpel et al. 2004). These considerations go beyond the confines of ecological risk assessment and involve environmental risk-benefit analysis (Bigler and Koll-iker-Ott 2006).

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